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THE THALATTOSAURIA

A GROUP OF MARINE REPTILES FROM THE TRIASSIC OF CALIFORNIA

By JOHN C. MERRIAM

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CONTENTS.

PLATES I–VIII.

INTRODUCTION 3
ORDINAL AND FAMILY CHARACTERS 5
OCCURRENCE AND AGE 5
MATERIALS AVAILABLE 7
GENERAL SKELETAL STRUCTURE 8
Skull 8
Facial Region 8
Fronto-parietal Region 10
Temporal Region 11
Quadrate, Suspensorium 12
Orbital Region 12
Palatine Region 13
Mandible 15
Dentition 16
Gnathic 15
Vomerine 17
Pterygoid 18
Function 18
Vertebrae 18
Ribs 19
True Ribs 19
Abdominal Ribs 19

May 5, 1905.

Limbs and Girdles 20
Pelvic Arch and Posterior Limb 20
Pectoral Arch 21
Anterior Limb 21

Habitat, Locomotion, Food 22

Affinities 23

Comparison with Similar or Related Types 23
Ichthyosauria 24
Parasuchia 26
Squamata 27
Proganosauria 28
Choristodera 28
Proterosuchus 29
Protorosauria 29
Rhynchocephalia 31

Conclusions 31

Generic and Specific Characterizations 33

Thalattosaurus 33
Thalattosaurus alexandrae 34
Measurements 34
Thalattosaurus shastensis 35
Measurements 35
Thalattosaurus perrini 36
Nectosaurus 37
Nectosaurus halius 38

INTRODUCTION.

In the course of the first investigation of the reptilian fauna of the Californian Triassic, the writer examined a peculiar jaw with a differentiated dentition which was exposed on a specimen loaned to him for study by Professor James Perrin Smith. This dentition was seen to resemble the figures of *Mixosaurus* published by E. Frass,[1] and in a preliminary note on the Ichthyosauria of the Californian Triassic[2] it was referred to that genus. Later preparation revealed the presence of other parts of the skeleton and showed a structure different from that of any Ichthyosaurian. This form was therefore not included among the Ichthyosauria described later from the Californian Triassic.[3]

During the field seasons of 1902 and 1903, expeditions from the University of California carefully worked over the greater portion of the Triassic limestone exposures in Shasta County, and made special efforts to secure material from which a satisfactory determination of the affinities of the unknown form could be made. As the result of this work, a large collection of ichthyosaurian material was brought together and with it a considerable number of specimens representing the new group. The preparation of this material has in all cases been difficult and has necessarily proceeded slowly, but it has resulted in giving us a fair representation of the most important elements of the skeleton.

The acquisition of our knowledge of the Thalattosauria has been made possible through the generous assistance of Miss A. M. Alexander, who has not only contributed the financial support of the field work, and in part also of the preparation of the material for publication, but was herself the discoverer of the specimens which furnish the greater part of our knowledge of the fundamental skeletal structure of the representatives of this group.

Acknowledgments for valuable services in connection with this investigation are also due to all the members of the University of California field parties which have worked on the Triassic limestones. To Professor James Perrin Smith I am under obligation for the information which led to the first exploration of the Shasta limestones in search of saurian remains, and for the loan of a valuable type specimen. To Mr. E. L. Furlong I am especially indebted for very efficient assistance extending through every stage of the work, from the collection of the specimens to the final preparation of the material for study. Dr. T. W. Stanton has loaned an important specimen for study and description.

1 E. Frass, Ichthyosaurier d. deutschen Trias & Jura Ablag., Pl. III, figs. 1–4.

2 Science, n. ser. v. 15, p. 411.

3 See Triassic Ichthyopterygia, Bull. Dept. Geol. Univ. Calif. v. 3, no. 4, p. 85, *Dentition*.

While preparing this report, some weeks were spent in examining typical specimens of forms in related groups. For favors in connection with the study of such material, the writer would express his most sincere thanks to the following gentlemen: Professor S. W. Williston, Dr. A. Smith Woodward, Dr. C. W. Andrews, Dr. E. Frass, Dr. F. von Huene, Professor E. Koken, Dr. Louis Dollo, Professor Henry F. Osborn, Dr. Lortet.

University of California,
March, 1905.

Superorder DIAPTOSAURIA.

Order THALATTOSAURIA.[1]

Marine saurians with abbreviated propodial and epipodial limb segments, elongated facial region, and median external nares. Skull with superior and lateral temporal openings and a pineal foramen. Prevomers and pterygoids as well as jaw elements dentigerous. General structure of skeleton of the rhynchocephalian type.

The group is composed of specialized natatory forms known only from marine deposits. It stands in somewhat the same relation to the typical Rhynchocephalia as that which the Mosasauria bear to the Lacertilia. Evidently derived from a primitive land or shore Diaptosaurian, it has taken somewhat the same course in evolution as was followed later by the Mosasaurs.

Family THALATTOSAURIDAE.[2]

Skull elongated, with slender rostrum. External nares separate and not far in front of the orbits. Premaxillaries elongated and forming a large portion of the snout. Premaxillaries, maxillaries and dentaries sculptured on external surface. Superior and lateral temporal openings and pineal opening present.

Prevomers with two rows of heavy, low-crowned teeth. Pterygoids with four or more rows of curved conical teeth. Premaxillaries and anterior end of dentary with slender conical teeth. Posterior part of dentary generally with depressed or flattened teeth.

Vertebrae amphicoelous, neural spines generally high and slender. Dorsal ribs single-headed. Abdominal ribs present. Coracoid reniform, elongated antero-posteriorly. Scapula narrow. Humerus short, expanded distally. Radius and ulna about half the length of the humerus; radius with median constriction; posterior border of ulna convex, radial border concave.

OCCURRENCE AND AGE.

The material upon which the group described in this paper has been based was all obtained in exposures of the Hosselkus Limestone lying between Squaw Creek and Pitt River, in the northern part of Shasta County, California.

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1 J. C. Merriam, Bull. Dept. Geol. Univ. Calif. v. 3, no. 21, p. 420.
2 *Ibid.*

Specimens were found at numerous localities in the extensive outcrops of this limestone, but the principal collections were made at localities known as Smith's Cove, Bear Cove, Grassy Point and North Fork. The first three localities are all on Brock Mountain, at the southern end of the belt of limestone north of the Pitt. Smith's Cove[1] lies on the southwestern side of the ridge, Grassy Point[2] on the northwestern side, and Bear Cove[3] near the middle of the eastern side. North Fork[4] is a locality on the north fork of Squaw Creek and about two miles northwest of the Kelley Ranch.

The bones occur in practically all horizons of the limestone, but good material is more common, or at least more easily obtained, in the softer, slightly shaly layers well exposed at the localities mentioned.

The limestone section has been divided by Professor James Perrin Smith[5], on the basis of faunal distribution, into the upper or Spiriferina beds, middle or Juvavites beds and lower or Trachyceras beds. The softer layers, where the best specimens were obtained, belong in general to the lower or Trachyceras horizon. In the other beds the material seems to be much more fragmentary and little but loose bones or teeth was obtained.

In all cases the remains have been very firmly united with the black limestone matrix, and successful preparation was possible only with the aid of an electric engine. As the bones are black, as well as the matrix, it was in many cases impossible to trace their outlines until they had been moistened with hydrochloric acid and allowed to stand for some days. This treatment resulted in the appearance of a delicate blue tint in the bone, evidently due to the presence of the mineral Vivianite, making it possible to follow the lines of contact with little difficulty.

Associated with the thalattosaurian remains are numerous ichthyosaurian bones, a few selachian teeth, occasional ganoid scales, and great numbers of molluscan shells. There are also a few brachiopods, corals and echinoids. The most common of all forms are the cephalopods, which frequently make up a large part of the rock. In the more shaly layers they may be replaced by the lamellibranch genus *Halobia*. A list of the most characteristic genera would include the following: vertebrates,—*Shastasaurus*, *Delphinosaurus*, *Toretocnemus*, *Merriamia*, *Hybodus;* invertebrates,—*Tropites*, *Sagenites*, *Eutomoceras*, *Juvavites*, *Polycyclus*, *Protrachyceras*, *Tirolites*, *Arpadites*, *Arcestes*, *Orthoceras*, *Nautilus*, *Atractites*, *Halobia*, *Rhynchonella*, *Spiriferina*, *Cidaris*.

1 Sec. 11 and 12, T. 34 N, R. 2 W, Mt. D. Merid.

2 Sec. 35, T. 35 N, R. 2 W, Mt. D. Merid.

3 Sec. 34, T. 35 N, R. 2 W, Mt. D. Merid.

4 Sec. 1, T. 35 N. and Sec. 36, T. 36 N, R. 2 W, Mt. D. Merid

5 See Comparative Stratigraphy of the Marine Trias of Western America, Proc. Calif. Acad. Sci. 3d ser. Geol. v. 1, no. 10, p. 360.

The invertebrate faunas have been extensively studied by Professor Smith[1], and are referred by him to the Upper Triassic on the evidence of general striking similarity of the fauna to that of the Alpine Triassic of Europe, even in some cases to the point of identity of species. Also in the case of the Ichthyosauria, almost unquestionable evidence of late Triassic age is given in the stage of evolution or specialization of various parts of the skeleton. In general this is near the stage reached by the Ichthyosauria of the later Triassic of Italy. This is particularly noticeable in the structure of the limbs, girdles and vertebral arches.

The presence of innumerable cephalopods with brachiopods and corals, in a limestone containing for the most part but little argillaceous material, leaves no room for doubt that the deposit was formed in a fairly clear sea, into which there was but little drainage at this point. The reptilian forms which we find in these strata evidently belonged to the typical marine fauna of the late Triassic.

MATERIALS AVAILABLE.

The specimen which has furnished the most satisfactory information in this investigation is the type of *Thalattosaurus alexandrae* (No. 9085). Excepting the anterior part of the skull and portions of the limbs and girdles, the skeleton had long been exposed and was largely weathered away. The remaining parts include the anterior two thirds of the skull with a small part of one temporal region. Of the girdles and limbs there are present the scapula, coracoid, humerus, ulna, three bones which represent the lower part of the pelvis and possibly the femur, and some scattered ossicles which may be either carpals or phalanges. Of the vertebral column there are parts of about thirty vertebrae extending in an interrupted series from the head to the anterior caudal region. There are also numerous scattered true ribs and abdominal ribs.

Another specimen (No. 9084), certainly of the same species, shows a portion of the skull with good mandible and quadrate, also both humeri, a radius and several well preserved dorsal vertebrae.

Two other smaller skulls having the same size and form are also referred to *Thalattosaurus* but probably do not belong to the type species. One of them (*T. shastensis*, No. 9120) shows the inner side of the posterior half of a skull in good state of preservation. With it are several good vertebrae, limb bones, ribs, abdominal ribs and teeth. In the second specimen the posterior three fourths of the skull are present, fairly preserved but very difficult of preparation.

[1] *Loc. cit.*

A fourth skull, the type of *T. perrini*, shows the greater part of the mandible, maxillary and palatine, with portions of numerous other elements of the skull.

The type of the genus *Nectosaurus* consists of the posterior two thirds of a mandible with the frontals, parietals, a prefontal, a post-fronto-orbital and part of a quadrate. Several loose jaws, portions of skulls, vertebrae, ribs, etc. are also referred to this genus.

GENERAL SKELETAL STRUCTURE.

Skull.

PLATES I–VI.

Considerable parts of the head are shown in five specimens. In all of this material, excepting the type of *Thalattosaurus*, the skulls are small and the bones thin and difficult to prepare.

The skull in the type specimen was fortunately broken into four segments by wide vein-filled cracks. In preparation, these segments were separated so as to show all sides of the bones and the cross-sections of the skull. The sections have been of especial value, serving as checks in observations on the position and arrangement of the bones.

The restorations of the skull (Text figs. 1 and 2, and Pl. VI) were based on the type specimen. The temporal and fronto-parietal regions and a portion of the mandible are restored from *T. shastensis*.

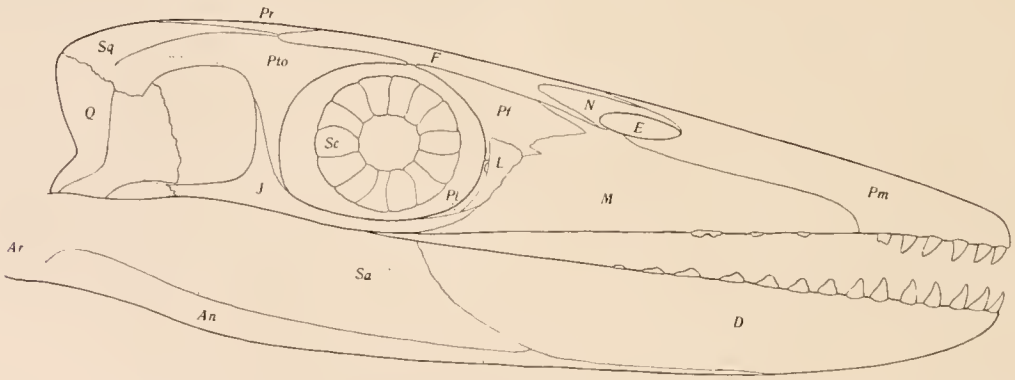


Fig. 1. *Thalattosaurus alexandrae*. Reconstructed skull, lateral view, × $^3/_8$. Pm, premaxillary; *M*, maxillary; *N*, nasal; *E*, superior nares; *F*, frontal; *Pr*, parietal; *Pf*, prefrontal; *Pto*, post-fronto-orbital; *J*, jugal; *L*, lachrymal; *Pl*, palatine; *Sc*, sclerotic ring; *Sq*, squamosal; *Q*, quadrate; *Ar*, articular; *Sa*, supra-angular; *An*, angular; *D*, dentary.

Facial Region.—As is shown in Plate I, the facial region of this skull is very slender. The snout was narrow, exhibiting some resemblance to that of the long-headed Mosasaurs.

Over a large part of the external surface of both maxillaries and premaxillaries, the rostral region has *sculptured* into it a series of pits and grooves. They run longitudinally on the premaxillaries but have in general a radial arrangement on the maxillaries. They appear also on the anterior portion of the lower jaw. While not so strongly impressed as in the Crocodilia or Stegocephalia they are nevertheless a characteristic feature of the skull in this group.

The *superior narial openings* were situated only a short distance in front of the orbits and are almost immediately above the inferior openings. They are separated by a heavy bar consisting of the nasals, frontals and premaxillaries. The superior openings are bounded on the external side by the nasals, the premaxillaries and apparently to a slight extent by the maxillaries. Anteriorly they are closed by the premaxillaries. In the type of *Thalattosaurus* there are also present certain peculiar elements which have somewhat the appearance of anterior prolongations of the prefrontals rising along the anterior margins of the openings. The character of these elements is, however, somewhat doubtful.

The greater portion of the snout is formed by the *premaxillaries*, which extend back to form part of the boundaries of the narial openings. The needle-like posterior ends reach back of the nasals and are thrust between the median anterior prolongations of the frontals. In the cross-sections (Pl. II, figs. 1*a*, 1*b* and 1*c*) the premaxillaries are seen to be distinctly separated. At section *c* (Pl. II, fig. 1*c*) each element shows two large dependent branches, one of which forms the external lateral wall of the snout, the other resting between upward prolongations of the prevomers. The alveolar margin is set with conical, slightly recurved teeth. The extreme anterior end of the premaxillary is not known, but judging from the extent to which this bone has narrowed anteriorly, as also from the character of the nearly perfect termination of the lower jaw, only a very small fragment is missing from the type specimen. The dentigerous portion of the premaxillary seems almost to have equaled that of the maxillary in length, though the inferior margin of the maxillary is longer.

In *T. alexandrae* the posterior end of the *maxillary* is considerably expanded vertically, reaching upward to the lateral prong of the frontal, with which it is folded into the prefrontal (Sec. *a*, Pl. I, fig. 1 and Pl. II, fig. 1*a*). The posterior part of the alveolar margin is not well preserved and it is not known whether it bore teeth. No part of this border appears to be pitted or grooved for the reception of teeth. On the anterior portion there are two prominences which seem to represent fangs from which the crowns have been almost entirely removed.

In *T. perrini* the maxillary dentition is very well shown excepting on the posterior portion of the jaw, which seems to have been edentulous. The teeth are sharply conical and are set in deep, distinct pits.

The *nasals* are clearly shown in the type of *Thalattosaurus*. They are not large and border mainly the median and posterior sides of the superior nares. They do not meet medially but are separated by the frontals and premaxillaries. The posterior ends rest between the forks of the frontals. A tendency toward separation of the nasals by extension of the frontals and premaxillaries is seen in many reptilian skulls, particularly in rhynchocephalian, lacertilian and sauropterygian forms, but such complete separation as is shown here is so rare that it may be considered an important character. The nearest approach to this structure is seen in the Sauropterygia.

In that group the nares are situated close to the orbits and are either median or subterminal. In all cases the premaxillaries form a large share of the snout. In the Nothosaurs the nasals have almost the same form as in *Thalattosaurus*, and the premaxillaries are thrust back between the nares though not in contact with the frontals. In *Pistosaurus* the premaxillaries touch the frontals, separating the nares and the small nasals. In *Plesiosaurus* the premaxillaries are in broad contact with the frontals. In *Dolichorhynchops*, recently described by Williston, the premaxillaries extend back to the parietals, separating even the frontals.

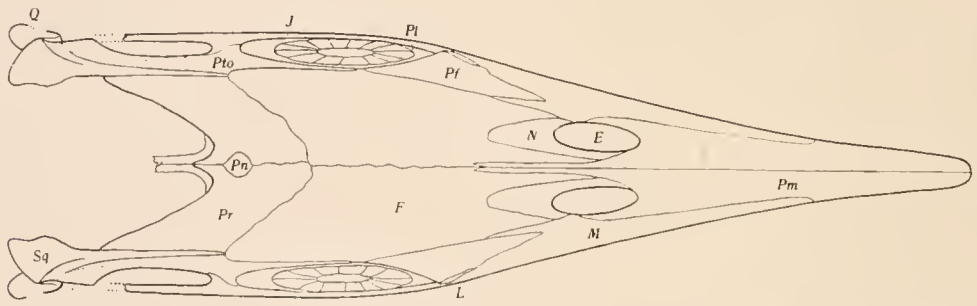


Fig. 2. *Thalattosaurus alexandrae*. Reconstructed skull, superior view, × $^3/_8$. *Pm*, premaxillary; *M*, maxillary; *N*, nasal; *E*, superior nares; *F*, frontal; *Pr*, parietal; *Pn*, pineal foramen; *Pf*, prefrontal; *Pto*, post-fronto-orbital; *J*, jugal; *L*, lachrymal; *Pl*, palatine; *Sq*, squamosal; *Q*, quadrate.

Fronto-parietal Region.—This region is particularly well shown in the specimen of *Thalattosaurus* represented in Plate III. Both frontals and parietals are distinctly paired and on both the superior surface is nearly smooth, being marked only by fine lines and pits. The *frontals* are relatively large. Their postero-external angles reach far back and partly clasp the anterior ends of the parietals. The anterior ends are deeply incised for the reception of the nasals. The median anterior forks extend forward as far as the middle of the superior nares, while the lateral forks reach almost if not quite to the outer border of the nares.

The *parietals* are much smaller than the frontals and are also separated by a median suture. A large parietal foramen lies between the two elements, but is a considerable distance behind the coronal suture. The posterior outer angles of the parietals are produced backward around the outer side of the superior temporal openings for more than half the length of the upper temporal arch.

In figure 2*a*, Plate IV, what appears to be the *squamosal* is seen to reach forward over the post-fronto-orbital to touch the frontal. If this is the normal relation of these elements, the outer border of the parietal is separated from the post-fronto-orbital. The median portion of the parietal is also produced backward as a slender arm and was probably in contact with the squamosal. The two posterior arms seem almost to have surrounded the upper temporal opening, giving to the skull an altogether peculiar character in this region.

Temporal Region.—The skulls appear to be characterized by the presence of both superior and lateral temporal openings. The *superior openings* are considerably smaller than the lateral. Judging from the specimen seen in Plate III, the posterior ends of the parietals were very slender and were dropped some distance below the level of the roof of the skull, so that the superior openings faced backward somewhat, as in *Belodon*. The anterior half or two thirds of this opening was enclosed by the parietal. The posterior boundaries have not been seen. They were probably formed by connection of the parietal and squamosal, though the supraoccipital may have intervened as seems to have been the case in *Sauranodon*.

The relatively large *lateral temporal openings* are seen in two specimens (Pl. III, fig. 2 and Pl. IV, fig. 2*a*). The boundaries are not perfect, even in the more nearly complete specimens, owing to the absence of the quadratojugal. In both instances, however, the jugal sends backward a long and strong process extending more than half the distance to the quadrate, and in one specimen the posterior end of this process is roughened as if from contact with a quadratojugal. Under these circumstances it would be difficult to believe that the *inferior bar* was incomplete. Should we assume that it was not complete it would be necessary to suppose that it is caught, as it were, in the process of breaking down, as no form losing the lower bar retains a posterior jugal process similar to that shown here. In reality there is hardly reason for supposing that the lower bar was even weak, as the posterior process sent out from the jugal is not stronger than it is here in many forms in which this arch is considered well developed.

The *upper temporal bar* is certainly made up to a great extent of the large post-fronto-orbital and the squamosal, as seen in Plate IV, figure 2*a*, with the addition of the outer posterior process of the parietal lying on the median side

of the bar. Even on the most complete specimens (Pls. III and IV) it has been impossible to determine certainly whether a prosquamosal is present or not, as the character of the bone is such that the sutures immediately above the quadrate are very difficult to determine. On what is taken to be the quadrate in a fragment of the temporal region of the type of *Thalattosaurus* (Pl. II, fig. 4) there rests a downwardly projecting arm which appears to be a part of an element that belonged to the lower side of the upper temporal bar. Evidently it extended down the outer wing of the quadrate, almost if not quite to the quadratojugal. The inner side of this bone, as also of that resting on the summit of the quadrate, is weathered away and it is not impossible that they were originally connected. If united, the squamosal must have had a form somewhat similar to that of *Sphenodon*. If separated, the lower element is apparently a discrete prosquamosal.

Quadrate, Suspensorium.—The *quadrate* is well shown in position in one specimen (Pl. III, fig. 2) and macerated out, though associated with the posterior end of the mandible and the cranium, in another (Pl. II, figs. 2*a* and 2*b*). It is of distinctly rhynchocephalian type, though approaching the lacertilian form in the development of a stronger posterior hook and a broad exterior wing. While the posterior side of the distal end is rounded upward the anterior side is distinctly flattened as if from contact with a quadratojugal. The presence of a high extero-lateral wing seems to preclude the possibility of there having been a fenestra between the quadrate and quadratojugal, as in the typical Rhynchocephalia, though there may have been a small opening near the distal end.

The relation of the quadrate to the temporal bones is such that it must have been immovable, in contrast to the general relations in the Squamata.

Orbital Region.—The specimens of *Thalattosaurus* show portions of large *sclerotic plates* in the orbits. They are similar in form to those seen in the Mosasaurs. In at least one instance a plate is deeply grooved on the margin, as occurs in forms in which the sclerotic ring is particularly heavy and strong.

In the boundaries of the upper side of the orbit the prefrontal and postfronto-orbital come so close together that the frontal hardly appears on the rim of the orbit. The posterior boundary is formed by the heavy ascending process of the *jugal*, and a single upper element evidently representing both the postfrontal and the postorbital. No evidence has been obtained which would tend to indicate the existence of a separate postfrontal resting above this bone. The apparent contact of the squamosal with the frontal might be interpreted to mean that a greatly reduced postfrontal is fused with the anterior arm of the squamosal, but until we have more definite proof of this it can be considered only as a mere possibility.

The *prefrontals* are large robust elements extending from the middle of the upper boundary of the orbit forward along the inner side of the maxillary.

The small *lachrymal*, extending over only a limited area of the face, is well shown in the type of *Thalattosaurus* (Pl. I, fig. 1, *L*). The lachrymal foramen is also distinctly seen here. In cross-section *b*, Plate II, figure 1*b*, *L* there is seen a peculiar element apparently distinct from the nasals, maxillaries, premaxillaries and prevomer. If such is really the case, this is probably an anterior prolongation of the prefrontal. This would, however, require an extraordinary enlargement of the anterior end of this bone, and further evidence is required before its relations can be satisfactorily determined.

Palatine Region.—It is in the palatine region that some of the most distinctive characters are seen in the members of this group. The general aspect here is of a primitive form in which the rostral region, and in it particularly the vomerine dentition, exhibits distinctive specialization.

The position and relations of the *prevomer* are best shown in the type of *Thalattosaurus* (Pl. I, fig. 2 and Pl. II, figs. 1*b* and 1*c*). It is here seen to lie largely between the maxillaries although reaching far forward along the rostrum. It is much elongated antero-posteriorly and has in general a sphenoidal form. So far as can be determined from the sections no median suture is present, though the structure may have been paired. From the median portion of the posterior end three laminae project backward, the median plate being much smaller than the others. On either side of these laminae the posterior margin shows a regularly rounded excavation, representing the anterior borders of the inferior nasal openings. The posterior plates evidently connected the prevomer with the palatines or the pterygoids. The palatal surface of the prevomer bears two long rows of teeth following the lateral margins. Posteriorly they are separated by quite a distance, but they approach each other near the middle of the bone and run parallel from that point forward.

In another specimen (Pl. V, figs. 2*a* and 2*b*), which was found separated from other skeletal remains, exactly the same form is shown. In the type of *T. perrini* (Pl. V, fig. 3) a part of a prevomer of the same general form is known. Fragments of several other specimens have been found to show corresponding structure. On all the specimens in which the anterior end of the prevomer is shown, the dentigerous portion of the bone is seen to bend downward sharply in the middle. In the specimen which was entirely separated from other bones of the cranium (Pl. V, figs. 2*a* and 2*b*), the drop is very pronounced and cannot be fully accounted for by distortion. A similar but less prominent bend is seen in the prevomer of *T. perrini*. Evidently the middle portion of the prevomer was produced downward somewhat, making the tooth row convex. The downward sweep is,

however, very pronounced and must have carried the vomerine teeth down to meet the low posterior teeth of the mandibular series.

The form of the prevomer seen here suggests the Rhynchocephalia, but differs from the known types in the character of the dentition. The broadened teeth of the posterior portion of the bone had possibly a function somewhat similar to that of the smaller vomerine teeth of the Choristodera; but they were much less numerous, were much larger, and were confined to the lateral margins of the palatal surface.

The *inferior narial* openings in *Thalattosaurus* are large and are situated almost immediately below the superior openings, the anterior borders being slightly anterior to the posterior borders of the upper openings. The external borders are formed in part by the maxillaries, as the anterior ends of the palatines do not appear to come in contact with the prevomer here in the manner in which they do in the Choristodera.

The anterior ends of the *palatines* are turned upward behind the narial openings and are deeply grooved to form the posterior walls of the nasal passages. As seen in section *a* (Pl. II, fig. 1*a*) the external border of the palatine is enfolded by the thin posterior end of the maxillary. In *T. perrini* (Pl. IV, fig. 3) the same relations are seen, only the narial opening is smaller. The median border of the palatine swings far around the nares here as if it had probably joined the prevomer broadly. The relations of the posterior and median sides of the palatine are only imperfectly known. The groove on the median side of the element (Pl. IV, fig. 3) is not such a contact as would occur if the corresponding element from the other side were met here. The presumption is that the anterior end of the pterygoid passing along the median border of the palatine was in contact with this surface.

In none of the skulls examined have there been found any indications of the existence of teeth on the palatine. In two specimens (Pl. III, fig. 3 and Pl. IV, fig. 3) this element can be seen in place and has been followed backward for a considerable distance without showing any traces of teeth, though they are well shown on other elements. The teeth shown close to the palatine on Plate IV, figure 3 are entirely distinct from it. They probably belonged to the pterygoid.

One of the most remarkable features of the type specimen of *Thalattosaurus* is a peculiar dentigerous bone which lay below the palatine region and above the separated rami of the mandible. Considering the position of the specimen, the character of the material, and the fact that no bones of other animals have been found in the matrix, there can be no reasonable doubt that it belongs to this skull. This bone (Pl. V, figs. 1*a*, 1*b* and 1*c*) is held to be the *pterygoid*. It consists of a narrow, thick plate, one border of which bore five rows of teeth. The

opposite margin of the plate supports a high, thin, triangular wing standing almost parallel with the tooth-bearing surface. The surface of this wing is marked on one side by radiating sculpture somewhat like that of the maxillary, excepting that it is largely in relief. The acute end of the wing is drawn out to a very thin edge. The broad end is considerably thicker and shows a deep groove where it was probably in contact with the quadrate.

The *pterygoid teeth* are in four rows with alveoli for a fifth. Unfortunately the crowns of nearly all were broken or weathered off and only the well preserved fangs remain. The teeth are all set in distinct pits and are inclined sharply toward the thickened end of the bone.

Considering that the palatine is edentulous and the vomerine teeth have specialized toward the low, broad type present only in a single row on each side, it is rather remarkable that the pterygoid teeth should be so numerous and evidently of the recurved, conical type. There is, however, no apparent escape from the conclusion that such is the case. Apparently the vomerine teeth served largely as crushers, while the pterygoid teeth assisted deglutition. The type of pterygoid represented here does not correspond exactly to any that has so far come to the writer's notice, but is not far removed from the type seen in some Rhynchocephalians.

In one specimen of *T. shastensis* (Pl. III, fig. 2, *Ep*) there appears to be a fragment of an *epipterygoid* in its natural position above the pterygoid. No ectopterygoid has been recognized.

Mandible.—(Pls. I, III and IV). Though no single specimen shows the whole of the lower jaw, overlapping portions of several exhibit the whole structure of both the inner and outer sides. The jaw is characterized by the sculpturing of the dentary, as shown in the type of *Thalattosaurus*, by the length of the angular, and by the prominence of the coronoid process.

The *dentary* does not appear to form the lower border of the outer side of the jaw excepting along the most anterior portion, owing to the extreme forward extension of the angular. The connection of the rami at the symphysis was loose and they have fallen away from each other in all of the specimens examined.

In *Thalattosaurus* the teeth upon the dentary extend back almost to the extreme posterior end of that bone, where they are low down on the inner side of the jaw. They are either set in depressions or appear to be fused to the jaw.

The extreme posterior end of the jaw is formed by the *articular*, which extends forward to be covered anteriorly by the splenial. The supra-angular is large and makes up the greater part of the posterior half of the jaw. The *angular* also forms a considerable part of the outer side of the jaw and ranges forward well toward the anterior end of the ramus. A large *splenial* covers

a considerable part of the inner side of the jaw. It extends back to a point below the middle of the coronoid and may reach forward almost, if not quite, to the symphysis.

The most characteristic feature of the mandible is the form of the *coronoid*. This element is broadly expanded over the inner side of the ramus and reaches with its upper border high above the supra-angular as a coronoid projection. The form of the coronoid is strongly suggestive of the Lacertilia, though it is approached in the true Rhynchocephalia. Particularly is this noticeable in the jaw of *Nectosaurus*, which taken by itself would appear unquestionably lacertilian.

Dentition.

The dentition is well shown in the type specimens of *Thalattosaurus*, as also in the lower jaw of the type of *Nectosaurus*, and more or less imperfectly in most of the other specimens. In addition to the jaw elements, the pterygoid and prevomer are dentigerous while the palatines are not known to have carried teeth.

Teeth of the Jaws.—The *insertion* of the teeth on the upper and lower jaws varies considerably within the group. In *Thalattosaurus* the teeth of both upper and lower jaws seem to rest in pits, which may be in elevated bases formed by the alveolar margin. In some cases they appear to be fused with the jaw bone. In *T. perrini* the teeth of both jaws rest in distinct pits. The depth of the pit and the general character of the insertion are to a considerable extent dependent on the form of the crown. The slender conical, anterior teeth are very deeply set in the jaws, while the pits for the low, broad-crowned, posterior mandibular teeth are much shallower. This may have been the case in *T. alexandrae* also, but the preservation of the anterior portion of the jaw of the type specimen has not permitted a satisfactory investigation of the insertion.

One of the diagnostic features of *Thalattosaurus* is found in the remarkable *differentiation* of the mandibular dentition. In *T. alexandrae* (Pl. 1, fig. 3) the crowns of the anterior teeth are slender conical with a slight lateral compression, while the most posterior teeth are very broad and nearly flat-crowned, resembling considerably the form of the teeth of *Placodus*, although very much smaller. The teeth in the middle portion of the jaw grade from the flat form to slender conical, through the gradual development of a tubercle on the antero-external portion of the crown. This elevation increases in size until it comprises the whole crown. Unfortunately the dentition of the upper jaws is not well known except on the anterior portion, where the crowns are conical as on the opposing portion of the mandible. Upon the maxillary, portions of two or three fangs are seen, but the crowns have been destroyed.

In *T. perrini* (Pl. IV, fig. 3) the dentition of the lower jaw shows again the conical anterior teeth with laterally compressed, low-crowned posterior teeth. The depression in the latter is, however, very much less than in *T. alexandrae*. In the upper jaw all of the teeth are conical. There do not appear to be any low-crowned or laterally compressed maxillary teeth. The most posterior portion of the maxillary was apparently edentulous and it is evident that the posterior vomerine teeth were in contact with the posterior portion of the mandibular dentition.

In the type of *Thalattosaurus* the perfectly preserved tip of the crown of an anterior mandibular tooth shows very faint wrinkles in the enamel. On the depressed posterior teeth the wrinkling of the enamel is more pronounced and in some instances a faint tuberculation is visible. A single loose tooth found with the jaws of this specimen has an elongated, somewhat compressed crown covered with numerous strong longitudinal striae.

Associated with the head bones of *T. shastensis* are several loose teeth showing the form very distinctly. In all of these the crowns are conical, but they vary considerably in length and thickness. The slender, curved teeth (Pl. IV, fig. 2*b*) are probably from the anterior portion of the jaws, and the shorter, heavier ones (Pl. IV, fig. 2*c*) from the middle region. The crowns are all supported on heavy fangs, such as are present in teeth inserted in pits. The enamel is marked with numerous fine, longitudinal wrinkles or striae somewhat finer than those on the corresponding teeth of *T. alexandrae*.

In no case has any evidence been obtained which would tend to show that the bases of the teeth have a folded internal structure as in the Ichthyosauria and Choristodera.

Vomerine Teeth.—In all specimens, so far as is known, vomerine teeth are present in only two rows, which are set upon the outer edges of the prevomer instead of next the median line. The rows converge anteriorly and near the middle of the prevomer they are very close together. From this point forward they run approximately parallel. In the posterior, diverging portions of the rows the crowns are very low and roughly triangular in cross-section. In the parallel portions the crowns are slightly higher. A very striking feature of the vomerine dentition is the downward sweep which it takes, the lowest point of the curve being at the place of convergence of the tooth rows. The teeth in this region seem to have come in contact with the low-crowned teeth near the middle of the lower jaw. The posterior vomerine teeth evidently met the posterior teeth of the mandible.

The vomerine teeth are set in depressions and where seen in a cross-section of the prevomer (Pl. II, fig. 1*c*) they are known to extend a considerable distance into

the bone. The enamel is ornamented with a large number of fine wrinkles radiating from the apex of the crown.

Pterygoid Dentition.—Closely set teeth were present in at least five rows on the heavy median plate of the pterygoid. They are of slender conical form and each is set in a distinct pit of considerable depth. Unfortunately the crowns have not been well preserved. They are all nearly circular in cross-section and the enamel seems to have been slightly wrinkled toward the base.

Function.—The dentition of the Thalattosaurs is evidently that of swiftly swimming forms feeding in a large measure upon fish. The character of the posterior mandibular and vomerine teeth of *Thalattosaurus*, indicating a crushing function, probably means that this type fed also in part upon some creature with a shell which could be easily crushed. Such forms would have been found in the numberless cephalopods of this epoch, and they doubtless furnished a portion of the food of the Thalattosaurs.

Vertebrae.

PLATE VII, FIGS. 1–5.

In the type specimen of *Thalattosaurus alexandrae* parts of over thirty vertebrae are shown. They represent the cervical, dorsal and anterior caudal regions. A number of loose vertebrae in a fair state of preservation are associated with other specimens.

In *Thalattosaurus* the centra of the *anterior dorsals* (Pl. VII, figs. 1 and 2) are nearly circular in vertical, transverse cross-section. The anterior and posterior faces are concave but not so deeply excavated as in the Ichthyosauria, the wall between the two faces representing more than half of the antero-posterior diameter of the centrum. The upper arches are rather slender and are not greatly thickened. The anterior margins are sharp. The posterior edges seem to be blunted or rounded. Strong zygapophyses are present. A characteristic feature of these vertebrae seems to be found in the closer attachment of the upper arches to the centra than we find in the Ichthyosauria. In this respect they resemble the vertebrae of the Plesiosaurs and Crocodiles.

An upper arch of *T. shastensis* (Pl. VII, fig. 4) shows the structure of the neurocentra better than in any other specimen. The spine is wider antero-posteriorly and is not so high as in *T. alexandrae*. Possibly this is due in this case to the arch having occupied a more anterior position than the arch of *alexandrae* figured (Pl. VII, fig. 1). The zygapophyses are large and strong and the facets well separated.

The ribs of *Thalattosaurus* articulate on a single wide apophysis, the upper portion (diapophysial) of which is situated above the middle of the centrum.

The surface of articulation is considerably narrowed in the middle but the apophysis is not seen to divide into distinct di- and par- apophyses. In the dorsal vertebrae examined, the uppermost portion of the rib head has been in articulation with the base of the neural arch.

In the *caudals* of *Thalattosaurus* (Pl. VII, fig. 3) the centra are somewhat angular in cross-section, though not greatly flattened laterally. The upper arches are very slender and relatively thick. Large and prominent zygapophyses are present. The faces are sharply separated and almost vertical in position. A slight elevation of the neural spines may indicate a little broadening of the tail. The structure of the vertebrae seems to indicate that the tail of *Thalattosaurus* was not a highly specialized sculling organ as in the Ichthyosauria and the Thalattosuchia. The propelling function may have been performed largely by the limbs as in the Plesiosauria. Evidence pointing in this direction is furnished by the bones of the pelvic arch, which are relatively large and robust for a swimming animal of this size.

Ribs.

PLATE VII, FIGS. 6 AND 7.

True Ribs.—Many fragments of ribs are present in the type specimen. In these the shaft is apparently about as heavy as in the Ichthyosaurs. The middle of the shaft is grooved on one side, the distal end is round in cross-section. In the single specimen in which the head is preserved but one articular surface is seen. In a specimen of *T. shastensis* showing several rib fragments associated with the bones of the head and the pectoral arch (Pl. VII, fig. 7) the shaft is rather heavy, is grooved anteriorly, and there is a single wide articular face as in *Shastasaurus*.

In the dorsal region the rib heads have articulated largely on the broad apophyses on the centra of the vertebra, but the uppermost portion rested also in part against the base of the upper arch.

Abdominal Ribs.—On one specimen (No. 9120) numerous abdominal ribs are present. They are long, and compared with the dorsal ribs are exceedingly delicate and slender. It has not been possible to distinguish between median and lateral pieces.

In the type specimen the lower portion of the skeleton with the abdominal ribs had been largely destroyed, but a single fragment apparently representing an abdominal rib is seen between the distal ends of the dorsal ribs.

Limbs and Girdles.

PLATE VII, FIGS. 8, 9 AND 10; PLATE VIII.

The pectoral and pelvic arches are both represented in the type specimen of *Thalattosaurus*. Apparently neither arch has been moved very far from its original position with reference to the remainder of the skeleton.

Pelvic Arch and Posterior Limb.—In the pelvic region of the type specimen there are parts of several bones evidently representing a portion of the pelvis and probably some of the elements of a hind limb. Only two of these bones are complete enough to permit identification. Corresponding to one of them there are in the collections two much better specimens (Pl. VII, figs. 8 and 10) giving a fair idea of its form. This element is larger than the other and differs from it somewhat in form. It exhibits characters which are not particularly definite and might permit its identification as either of the inferior elements of the pelvic arch or possibly as the femur. It is narrowed somewhat below the proximal end or head and is considerably broadened distally. The expanded anterior margin of the distal end is thin and slightly decurved. The distal portion is thickened, excepting in the middle of the end, and is excavated along the distal border. The proximal end is also excavated. On the more strongly concave side of the neck there is a small foramen in all three specimens.

This element shows some resemblance to a femur, and when first examined was thought to represent that element. It also resembles the pubis in the form of both ends, in the curvature of the shaft, and in the twist of the outer margin. The small foramen near the proximal end might occur behind a trochanteric elevation of a femur or in the pubis. If this is the femur it represents a type of extremity quite different from that seen in the anterior limb, the distal end being turned sharply backward and slightly upward. Propodial elements of this kind are not uncommon in natatory reptiles, but when present in the hind limb, the fore limb is usually, though not always, of a similar character.

The other element belonging in this region (Pl. VII, fig. 9) is again of somewhat indefinite form. It is quite similar to the first mentioned element but is smaller and shows a greater expansion of the median portion, producing a prominent wing. This bone might be either pubis or ischium but is probably the latter.

A fragment of another large element lying next the ischium may represent the ilium or the femur. It is nearly straight and appears to be almost circular in cross-section.

However we may interpret the elements which have been discussed, it is evident that at least one of them must belong in the inferior portion of the

pelvis, and that the characters of either or both of them are such as to show that the pelvis was not of the plate-like form usually seen in the primitive Diaptosauria.

Both of the elements described from the pelvic region of the type specimen are large compared with the coracoid, scapula and humerus. No matter how we interpret them, they show that the posterior limbs were possibly more powerful than the anterior, reminding us of the peculiarly specialized Thalattosuchia of Frass.

Pectoral Arch.—The pectoral girdle is represented by the coracoid and scapula. No clavicle or interclavicle has as yet been discovered. Several fragments of large bones associated with the pectoral girdle may represent one or both of these elements. The *coracoid* (Pl. VIII, fig. 1) is reniform and has somewhat the form of the coracoid in the ichthyosaurian genus *Merriamia* from the same horizon. It is, however, more distinctly reniform, having a sharply concave exterior margin.

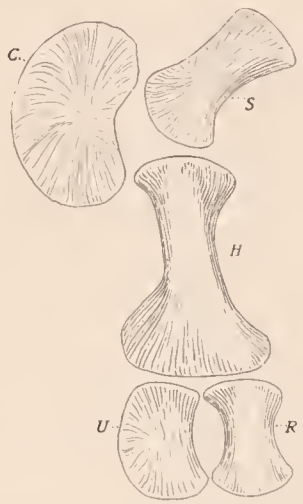


Fig. 3. *Thalattosaurus alexandrae*. A portion of the right pectoral arch and limb seen from above, × $^3/_8$. *C*, coracoid; *S*, scapula; *H*, humerus; *R*, radius; *U*, ulna.

The *scapula* (Pl. VIII, figs. 2 and 3) is comparatively narrow resembling that of the Crocodilians, Parasuchians, the later Ichthyosaurs, and most of the rhynchocephalian forms. It differs from that of the Triassic Ichthyosaurs in lacking the considerable distal expansion.

The structure of the pectoral arch, so far as known, seems more primitive than that of the Triassic Ichthyosaurs and is of distinctly rhynchocephalian type.

Anterior Limb.—Elements belonging to the anterior limbs are found in the type and in two other specimens. In the type the humerus and the ulna are present. In another specimen both the humeri are well preserved and with them is a nearly perfect radius.

The *humerus* (Pl. VIII, figs. 4*a* and 4*b*) is considerably expanded dorsoventrally at the proximal end through the development of a very heavy pectoral ridge extending to the middle of the shaft. The distal end is greatly broadened, its width equaling two thirds the length of the bone. In either inferior or superior view the middle of the shaft appears more slender than is actually the case, owing to the fact that the expanded ends are twisted at right angles to each other. Both the proximal and distal ends seem to be deeply excavated, and evidently supported large cartilaginous caps. In one specimen (Pl. VIII, fig. 4*b*)

a small foramen is seen near the distal end of the pectoral ridge. Although it is quite small it probably represents an epicondylar foramen.

The humerus of *T. shastensis* (Pl. VIII, fig. 8) is perhaps a little more slender than in *T. alexandrae*, but is imperfectly represented in the figures, as it is considerably weathered.

The *radius* (Pl. VIII, fig. 5) is shafted, but shows considerable distal and proximal expansion. Its length is about one half that of the humerus. The *ulna* (Pl. VIII, figs. 6 and 7) is convex posteriorly and concave anteriorly, showing no median constriction.

Several rounded ossicles resembling the phalanges of *Baptanodon* have been found associated with the limb and arch bones of the type specimen. Undoubtedly they represent carpals or phalanges, and there is a possibility that some at least are phalangeal elements.

The *type of limb* represented in this form is that of an aquatic animal, as is shown particularly in the extreme shortening and broadening of the humerus and of the epipodial bones. Such indications as are given in the possible character of the phalanges would also point in this direction. The specialization of the limb is greater than that in the Proganosauria, Choristodera or Parasuchia. It can perhaps be best compared with that of the Plesiosaurs or with the Triassic Ichthyosaurs. The humerus is, however, a little more slender medially than in the Ichthyosaurs. If the rounded ossicles are really phalanges, it is evident that the limb was no longer serviceable to any extent for land or shore locomotion but had become the specialized paddle of a purely aquatic type.

HABITAT, LOCOMOTION, FOOD.

The remains of Thalattosaurs are known only in purely marine deposits containing little or no material of terrestial origin. They are associated with a fauna consisting of numerous forms, both vertebrate and invertebrate, which are not known to have existed away from marine areas. In the structure of the skeleton we find the abbreviated and broadened proximal segments of the limbs, the slender snout with prehensile terminal teeth, and the median superior nares, indicating a purely aquatic type. There can scarcely be room for doubt that the Thalattosaurs as a group were typical marine forms.

The larger and more specialized species comprised in the genus *Thalattosaurus* were strictly natatory. They may have visited the shore but, like the Plesiosaurs, were better fitted for swimming than for crawling. Of the smaller *Nectosaurus* we unfortunately do not know the limbs. They may have been considerably less specialized than in the other genus, and the animal to a corre-

spondingly greater degree a shore dweller. *Nectosaurus* is, however, found in the same deposits with the other forms and appears to be as common as the others; so that it is safe to consider it as having passed the greater part of its life away from the shore.

From what we know of the vertebral column of *Thalattosaurus* it appears that the animal had a relatively short neck and a long dorsal region, the proportions being near those in the vertebral column of some Mosasaurs. Only the anterior portion of the caudal region is known. The slender, rounded neural spines with well developed zygapophyses seen here are not such as commonly appear in forms with a highly specialized sculling tail, and it is hardly probable that a caudal fin of large size was developed.

The anterior limbs evidently formed paddles of moderate size. The posterior pair may have been larger, in compensation for lack of a strong sculling tail. It is, however, possible that as in *Geosaurus* the hind limbs were not typically natatory and that the distal end of the tail was vertically expanded.

No specimens have yet been found which are well enough preserved to show any remains of the stomach contents, and we have no definite evidence concerning the food of the Thalattosaurs, more than is furnished by the general structure of the animal. The character of the paddles, the form of the skull, and the presence of slender prehensile teeth in the terminal portions of the jaws would indicate that they fed in part upon some swiftly moving prey which was caught by a quick snap of the jaws, deglutition being assisted by the curved teeth of the pterygoid. The heavy vomerine and posterior mandibular teeth may have been used for crushing the light shells of ammonites, which existed in vast numbers in the same seas.

AFFINITIES AND SYSTEMATIC POSITION.

As would be expected in forms occurring in the Triassic, the Thalattosauria exhibit many features which are generally considered as primitive. Among these are the biconcave vertebrae, single-headed ribs, well developed abdominal rib plastron, narrow scapula, plate-like coracoid, sculptured jaw elements, strong vomerine and pterygoid dentitions, and the presence of a parietal foramen. It is, however, by no means a primitive type, but is really one of the more specialized of the reptilian groups of the Triassic. Peculiar or specialized characters appear in the structure of the limbs, in the rostral region of the skull, in the position of the narial openings, in the relations of the nasals and premaxillaries, in the character of the parietals, and in the nature of the dentition.

Owing to the considerable degree of specialization of the particular kind which we find in this group, it would almost necessarily be true that any order

in which it could be placed would be comprised mainly of aquatic forms. Its relationship to any other than an aquatic group will probably be a weaker bond than ordinal affinity, and very close similarity must be sought in some of the natatory types.

The characters of the Thalattosaurs are such as to bring them into more or less definite relationship to a considerable number of groups. In some cases this is due to similar adaptation. To several quite different groups they show true affinities of nearly the same degree, indicating relationship through a common ancestral type or group from which they have all originated. The most important resemblances and affinities are discussed somewhat in detail before presenting the conclusions reached through these comparisons.

Ichthyosaurian Affinities.—The Thalattosaurs inhabited the same seas with a large group of Ichthyosaurians and showed much the same kind of adaptation carried also to a high degree. The Ichthyosaurs are generally held to be nearly related to the Rhynchocephalia, and the Thalattosaurs are evidently near relatives of that group. Under these circumstances we should expect to find the Ichthyosaurs and Thalattosaurs showing similar structure and giving evidence of near relationship.

In the extremities, where adaptation to aquatic conditions is most readily and distinctly expressed, we find both forms exhibiting the typical natatory type. In the Ichthyosaurs the propodial and epipodial elements show a somewhat greater degree of abbreviation. Unfortunately we do not as yet know the character of the terminal portions of the paddles in the Thalattosaurs and can make no comparison here. As far as is known, the ichthyosaurian paddles seem to have attained a slightly higher degree of specialization.

In the vertebrae of the two groups there are considerable differences in the character of the neural spines, in the zygapophyses and in the attachment of the upper arches to the centra. The difference in form is particularly noticeable in the anterior caudal region. The pectoral girdles are somewhat similar, but as far as is known the pelvic arches are quite different.

In the skull we find the nares occupying much the same position in both groups, and the premaxillaries are elongated in both. In the Ichthyosaurs the premaxillary elongation is extreme and the maxillaries are not only relatively small but seem actually to have suffered reduction. Distinctive skull characters separating the Ichthyosaurs widely from the Thalattosaurs are noted in the absence of an inferior temporal opening and of a coronoid elevation, the separation of the postfrontal and postorbital, the enormous size of the nasals and their different relations to the premaxillaries, the different relations of the parietals to the small frontals and to the superior temporal openings, a different structure

in the palatine region, the lack of vomerine and pterygoid teeth, and the isodont or only slightly differentiated character of the gnathic dentition in all the known species of this epoch.

Some of the structural differences separating these two groups are doubtless to be correlated with difference in habits; in other words, they may be ascribed to somewhat different kinds of adaptation. The Ichthyosaurs were largely fish eaters. They therefore had no great need of a heavy vomerine dentition. In the same way the presence of a strong coronoid projection on the thalattosaurian jaw may be correlated with somewhat increased muscular power used in crushing with the broad teeth of the prevomer and of the posterior portion of the dentary. Other differences may be due to great increase in the size of the orbits in the Ichthyosaurs, although this may be considered as due to better opportunity for increase in size in that group owing to fundamental difference in the original structure of the skull.

These facts are particularly significant when we consider their bearing on questions concerning the origin and relationships of the Ichthyosaurs. If the Thalattosaurs and Ichthyosaurs were both derived from the primitive Diaptosauria and were both typical marine forms following somewhat similar lines of adaptation, why are they so different? With similar environmental conditions we would expect but little divergence. It is evident that in this case we have one of the following possibilities: 1. The Thalattosaurs and Ichthyosaurs have come from the same stock but have followed quite different lines of adaptation: 2. They have come from the same stock and have followed only slightly different lines of adaptation, but have, one or both, been in existence for a very long period: 3. They have originated in different groups.

Concerning the first possibility—there is reason to believe that the groups differed somewhat though not greatly in food habits, but that in a broad way the kind of adaptation was the same. It was such as would generally tend to produce a certain degree of convergence. The kinds of adaptation we should presume to differ less than among the Cetacea, while the structural differences are as great or greater than we find produced in not less than four periods of evolution in that more rapidly living aquatic group.

Regarding the second case—we unfortunately know as yet but little concerning the early history of either group. Thalattosaurs are known as early as the beginning of the Upper Triassic, and the oldest Ichthyosaurs which we know are found in the lower part of the Middle Triassic. The Ichthyosaurs certainly appear to be somewhat more specialized than the Thalattosaurs and are presumably somewhat older, so that we could imagine a slight difference in adaptation acting through a long period as having resulted in the production of these

very different types out of the same stock. The Ichthyosaurs may have taken to the sea earlier, and the Thalattosaurs have originated from a later and therefore somewhat different phase of the same group. On the other hand the development of such differences as we see here must have required much time, and it may well be questioned whether the time of origin of the Ichthyosaurs may not date back so far that it would be straining a point to call its ancestors Diaptosaurian or even Diapsidan.

The remaining situation, in which we would have the two groups converging from fundamentally different stocks, seems in many respects the most natural relation. At any rate, the two groups must be considered as widely separated, and neither may be judged to be ancestral to the other. If they are not closely related and it should appear that of the two the Thalattosaurs are nearer to the Rhynchocephalia, we may perhaps reasonably question the rhynchocephalian or diaptosaurian origin of the Ichthyosaurs.

Parasuchian Characters.—The general skull structure of the Thalattosaurs has a certain degree of resemblance to that in *Belodon*, particularly in the rostral and temporal regions. The position of the nares is similar, as also the general form of the premaxillaries and maxillaries, though the premaxillaries do not separate the nasals and reach the frontals. The superior temporal openings are similarly situated low down between the upper temporal bars, and the parietals bound the anterior side to a greater extent than is usual. There is also some similarity in the structure of the palate, and the gnathic dentition of *Belodon* is not unlike that of *Thalattosaurus perrini*. Taken as a whole, however, the two skull types are very dissimilar. The superior nares of *Belodon* are in the large nasals; the premaxillaries do not reach back to the frontals; large antorbital vacuities are present; the lachrymals are large, while the prefrontals, frontals and parietals are relatively very small; the postorbital and postfrontal are separate; there is no pineal foramen; the form of the quadrate is very different from that of *Thalattosaurus;* the palatine borders the inferior nares externally; the coronoid is small and inferiorly situated; there are no teeth on the prevomers or pterygoids; and there is a large mandibular vacuity. These differences together with the total dissimilarity in the structure of the vertebrae, ribs and limbs show that the two groups are ordinally distinct. The general outlines of the structure in both are those of the primitive diapsidan Reptilia. Both are aquatic types and to a slight extent this has tended to bring them nearer together. The possibilities of evolution in the *marine* Thalattosauria were, however, much greater and also specifically different from those open to the *fresh water* Parasuchians, and the result of specialization has been the production of very different forms. As different as these two are, it may be noted that they are at least as near together as the Thalattosaurs and the Ichthyosaurs, although the latter are marine.

Relationship to Squamata.—Although the Thalattosaurs evidently possessed two temporal openings, with a complete lower temporal bar, their resemblance to the lacertilian and mosasaurian branches of the Squamata are so prominent as to demand consideration of possible relationship to them. The general aspect of the mandible is that of a representative of the Squamata, though it is also approached in the Rhynchocephalia. The form, situation, and prominence of the coronoid are such that the posterior portion of the jaw taken alone could scarcely be considered as other than lepidosaurian.

On the superior side of the skull there is a noticeable similarity to the Mosasauria. In both the Thalattosaurs and Mosasaurs the rostral region is narrow; it is generally somewhat elongated and acute terminally. The nares are set well back and the premaxillary is produced posteriorly as a stem or bar which meets the frontals. There are no discrete nasals in the Mosasaurs and they are generally supposed to be united with the posterior end of the premaxillary bar as in *Varanus*. Should it appear that they have been lost and the fronto-premaxillary connection be immediate, the structure in this region would be very similar in the two groups.

In the posterior part of the Mosasaur skull the broad frontals are often partly arched around the anterior ends of the parietals as in the Thalattosaurs, while the postfrontal and postorbital have partly united. So far as can be determined, there is room to suppose that the upper portion of the temporal region may not differ greatly in the two groups. The quadrate of the Thalattosaurs is in general of rhynchocephalian type and the widely extended anterior wing is not seen in the Squamata, but the presence of a strong external wing and the incipient development of a posterior hook make it begin to show resemblance to the type seen in the Mosasaurs and Lizards.

In the characters of the limbs and arches there is much that is similar. The vertebrae and ribs differ, but perhaps not so fundamentally as would appear from superficial examination.

On the whole the resemblance to the aquatic Squamata is very striking; but it can not overbalance such characters as the evident presence of a lower temporal arch, the existence of a strongly developed vomerine dentition, an immovably fixed mainly rhynchocephalian quadrate, abdominal ribs and very primitive vertebrae.

While it is not possible to place the Thalattosaurs in the Squamata, as that group is at present defined, it is not improbable that the primitive Lacertilians were closely related to or derived from the land or shore forms from which the Thalattosaurs were derived. Adaptation to aquatic life would tend to make the Thalattosaurs take on rapidly a certain set of characters which would appear

again in the Mosasaurs. This specialization would at the same time take the Thalattosaurs out of the direct line of evolution. It is to be noticed in this connection that the smallest and least specialized form, seen in *Nectosaurus*, is nearer the Lacertilia than the larger and more specialized *Thalattosaurus*.

In *Paliguana* Broom, of the South African Triassic, we have represented an undoubted Lacertilian with the lower temporal arch absent and only a minute process projecting from the posterior side of the jugal. The quadrate is typically lacertilian as are also the relations of the elements in the upper temporal bar. This form shows that the characteristics of the Squamata were expressed very early and makes more probable the discovery of lacertilian tendencies in early diaptosaurian groups.

Relationship to the Proganosauria.—As possible close relatives of the Thalattosaurs, the Proganosauria claim especial notice; being a group of rather primitive aquatic forms having affinities with the Rhynchocephalia and occurring earlier in geological time than the Thalattosaurs, and therefore possibly ancestral to them. Unfortunately the part of the thalattosaurian skeleton of which we have the best knowledge, viz. the skull, is the most imperfectly known part in the Proganosauria. Osborn considers the skull probably double-barred, though the structure of the temporal region is as yet unknown. The position of the superior nares and the structure of the palate are likewise unknown. Teeth are present on the roof of the mouth on what are supposed to be the palatines, while in the Thalattosaurs they are absent from the palatines, and present on the prevomer and pterygoids. The skull is considerably longer and more slender in the Proganosauria and the long, slender teeth are more numerous.

In the structure of the better known parts of the skeleton of the Proganosaurs the separation is wide. The small centra and greatly expanded upper arches of the vertebrae and the peculiar narrow-headed ribs of the Proganosaurs stand in strong contrast to the relatively small upper arches and the broad-headed ribs of the Thalattosaurs. In the pectoral girdles of the two there is some similarity excepting in the scapula. The plate-like pelvis of the Proganosaurs is much more primitive than that of the Thalattosaurs and the limbs of the former have not gone nearly so far in specialization, particularly in the shortening and broadening of the epipodial elements.

Relationship to the Choristodera.—The aquatic diaptosaurian forms included in the Choristodera resemble the Thalattosaurs mainly in that they are aquatic and have rhynchocephalian affinities. Here, as in the Thalattosaurs, there is a vomerine dentition but the teeth are small, very numerous, of an entirely different form, and are set in several rows. The pterygoid dentition is also different and the palatines bear teeth. The Choristodera are farther distinguished from

the Thalattosaurs by the more slender snout, the terminal position of the nares and the correspondingly different structure of the rostral region, the absence of a pineal foramen and of a coronoid process, the robustness of the ribs and the bicipital articulation of those in the anterior dorsal region, the different form of the elements in both pectoral and pelvic arches, and the relatively but little specialized limbs.

In the lengthening of the snout the Choristodera are more specialized than the Thalattosaurs, but the terminal position of the external nares shows the kind of specialization which we find mainly in aquatic reptiles belonging in fresh water, while the position of the nares in the Thalattosaurs is the form of specialization seen generally in marine types.

When we consider along with other things that the Choristodera are in some respects much less specialized than the Thalattosaurs, and that they occur two geological periods later, it is evident that they are not closely related.

Resemblance to Proterosuchus.—Some interesting resemblances to the Thalattosaurs are shown in *Proterosuchus* recently described by Broom.[1] This important form is known only from the anterior portion of a skull recently discovered in the Karoo beds of Tarkastad, South Africa. In it we find dentigerous prevomers and pterygoids with edentulous palatines. The prevomers reach back to meet the pterygoids broadly. On the upper side of the pterygoids are high, thin vertical plates. The characters of this form amply justify its determination by Broom as "a primitive Rhynchocephalian which shows a considerable degree of specialization along a line which gave rise to the crocodiles. . ."

The combination of characters found in *Proterosuchus* is in some respects similar to that seen in *Thalattosaurus*, and as is shown by Broom for *Proterosuchus*, the palatine region exhibits a general resemblance to that of *Procolophon*. In other characters, as in the presence of large antorbital vacuities, the anterior position of the external nares, the position of the internal nares farther forward and separated by the main bodies of the prevomers, in the absence of a coronoid process, and in the large size and heavy fangs of the slightly differentiated teeth, *Proterosuchus* shows itself to be quite different from *Thalattosaurus*. The resemblance exhibited by these forms is evidently in the main due to their approximation to the type of the primitive Rynchocephalia. Such similarities as we find are not sufficient to permit our including them both in the same order. In adaptation to aquatic conditions *Proterosuchus* might have led to some such forms as the Parasuchians, while the Thalattosaurs stand as a type very different from this order.

Relationship to the Protorosauria.—Very close affinity with any of the forms

[1] R. Broom, Ann. South African Mus. v. 4, art. 7, p. 159, pl. XIX. Nov. 1903.

in this order is precluded by the totally different structure and function of the limbs, the character of the pelvis, and to a considerable extent also of the lower jaw and the facial region.

The skull of *Palaeohatteria* differs from that of the Thalattosaurs in the terminal position of the superior nares, the small and short premaxillaries, large maxillaries and lachrymals, very large nasals, separate postfrontal and postorbital, absence of coronoid or at least of a prominent coronoid projection, and in the presence of large prehensile teeth on the posterior portion of the jaws. It might be presumed that the greater number of these differences could be brought about by retrogression of the narial openings with corresponding enlargement of the premaxillaries, in the evolution of an aquatic form from a type originally like *Palaeohatteria*. There are, however, few real similarities connecting *Palaeohatteria* and the Thalattosaurs which would not at the same time show affinities with the majority of the older diapsidan orders. While such modification may be considered possible, there is nothing to show that it has actually occurred.

The relationship to *Protorosaurus* is hardly nearer than to *Palaeohatteria*. The limbs, girdles and vertebrae are very different, and the skull is not more similar. The facial region in some respects seems to present a stronger resemblance than to *Palaeohatteria* and if, as Seeley has suggested, the openings immediately in front of the orbits in *Protorosaurus* are really the superior nares, there would be an important feature common to the two. The nasals are, however, very large, reaching far forward as in the Ichthyosaurs, and the premaxillaries appear to have no posterior stem. In the palatine region we find the prevomer long and slender, and the palatines swinging around the narial openings and coming into broad contact with the prevomers in front of the nares as well as behind them.

Evidently no close affinities are to be found with the Protorosauria, and while we must suppose the Thalattosaurs to be derived from Permian land or shore forms, it would not be possible to unite them with this group or even to consider the Protorosauria as the ancestral type. As has been shown by Seeley, Nopcsa, Osborn and others the trend of evolution in the Protorosauria was already decidedly toward the development of specialized land forms, as seen in the Dinosauria.

The Thalattosaurs are probably derived from land forms, as is evidenced by the character of the pelvis and of the neural spines of the vertebrae. The Protorosaurs probably come nearer than any other group to this primitive type, but are not themselves the ancestral forms which we seek.

Relationship to the Rhynchocephalia.—In a large number of the skeletal characters, strong similarities to the Thalattosaurs are found in various members of the Rhynchocephalia. In the general plan of the skull there are many points of resemblance, and the uniformity of this resemblance throughout the various parts is particularly noticeable. In some respects we find in the Rhynchocephalia approximations to thalattosaurian characters not seen elsewhere.

In the superior temporal region the similarity of *Sauranodon* and *Pleurosaurus* to the Thalattosaurs is evident. The parietals here extend around the anterior ends of the upper fenestrae as in *Belodon*, and in both of these genera they meet the squamosals on the outer side of the upper temporal openings.

In the structure of the arches and ribs many common characters are found, although the vertebrae are not closely similar. The similarity of the more slender pelvic elements is particularly noticeable, being closer than between the thalattosaurian elements and the primitive plate-like pelvis of the Protorosauria and Proganosauria or the broad pelvic elements of the Choristodera.

As discriminating characters, we find that no true Rhynchocephalian possesses a vomerine or pterygoid dentition or shows the degree of adaptation of the limbs and skull to aquatic conditions that we find in the Thalattosaurs. No member of this order has such highly specialized limbs and in none do we find the thalattosaurian structure of the rostral region. *Pleurosaurus* and *Acrosaurus* were aquatic forms, but the limbs were only slightly modified. The structure of the nasal region in *Pleurosaurus* approaches that of the Thalattosaurs but does not appear to be the same. Moreover, in *Pleurosaurus* where we find some of the closest resemblances, the structure of the lateral temporal region appears very different. From Lortet's figures[1] it would seem that there is no lateral temporal vacuity here. Such was also the impression obtained by the writer in a hasty examination of his specimen.

As all of the Rhynchocephalia which we have for comparison are much younger than the Thalattosaurs, and are all in many respects less specialized, it is useless to attempt to place them in any very close relationship to the Thalattosauria. It is probable that they are derived from a persistent land or shore type from which the Thalattosaurs are an early offshoot.

Conclusions.

From the comparisons that have been made, it is evident that the Thalattosaurs are to be considered as an independent group. The orders with which

[1] Rept. Foss. du Bassin du Rhone, 1892. Pl. VIII, figs. 1 and 2.

they have most in common are either those comprising typical aquatic forms or those in which rhynchocephalian characters are very prominent. Even where we have the characters of an aquatic animal developed in a form of the rhynchocephalian type, we fail in every instance to find closer affinity than the bond between the Mosasauria and the Lacertilia or that between the Choristodera and the Rhynchocephalia.

During the period in which the Thalattosaurs flourished there were three other important groups of marine reptiles in existence. These were the Nothosaurs, Ichthyosaurs and Placodonts, none of which were closely related to the Thalattosauria. Of the older reptilian orders, the Protorosauria and Proganosauria are nearest the Thalattosaurs. The first of these comprises terrestrial types with quite a different structure and showing already in the Permian that the tendency of their evolution was toward highly specialized land forms. The Proganosaurs, also of the Permian, exhibited a different type of evolution in the skull, ribs and vertebrae, and had much less specialized limbs.

Of the younger orders the Choristodera and Rhynchocephalia show noticeable similarity to the Thalattosaurs in their fundamental skeletal plan. The affinity with the Choristodera is on the whole weak, as the skull, arches and limbs are decidedly different. They represent a distinct aquatic type which must reach back to the primitive Diaptosauria for a true expression of its affinity with the Thalattosaurs. The Rhynchocephalia s. str. as shown in the numerous types ordinarily classed in it show more real kinship with the Thalattosaurs than most of the other orders. Affinities are expressed in varying degrees in *Sphenodon*, *Homeosaurus*, *Pleurosaurus* and *Sauranodon*. It is, however, to be doubted whether all of these forms should be grouped in one order. In the possession of numerous peculiar characters, both primitive and specialized, and particularly through the group of characters which has arisen owing to the higher degree of adaptation to aquatic conditions, the Thalattosaurs show themselves distinctly separated from the true Rhynchocephalia.

The resemblances to the Squamata are striking. They are evidently founded in a large measure on parallelism, but may also be due to close affinity between the primitive Thalattosaurs and the particular group in the primitive Diaptosaurs from which the Squamata originated.

The Thalattosaurs represent an early adaptation to marine conditions of that division of the Reptilia which has persisted in measurably primitive form in the Rhynchocephalia. During the early history of that group it gave rise to a numerous company of forms taking quite divergent paths in their evolution. Of the older orders only the Proganosauria were aquatic. They appear, however, to have been limited to fresh water. The Thalattosaurs are evidently the

marine representatives of this great rhynchocephalian or diaptosaurian group. In accommodation to marine conditions their specialization toward the natatory type was carried farther than it would naturally go in forms living in the more narrowly circumscribed bodies of fresh water. In sea forms a continued or sustained existence in the water, and even some distance away from the shore, was probably advantageous. Such a tendency would necessarily result in the evolution of the only type of extremity that would be serviceable; namely, the paddle. In bodies of fresh water where the shore is in general easily accessible the functions of the limbs would be divided between crawling and swimming.

Of the seven orders tentatively placed in the Diaptosauria by Osborn none are composed of typical natatory, marine forms. It would have been remarkable had there not been developed in the adaptive expansion of this group just such a type as is represented here. In the relation of the Thalattosaurs to the other diaptosaurian orders we find a situation similar to that in the Squamata, the Thalattosaurs showing the same kind of adaptive specialization away from the primitive Diaptosauria that the Mosasaurs have exhibited with relation to the primitive Lacertilia.

GENERIC AND SPECIFIC CHARACTERIZATIONS.

In general, the structure of the known specimens indicates close relationship of the forms which they represent. There is, however, a certain degree of variation, particularly of the dentition and limbs, which is best expressed by separating them into two or more genera.

THALATTOSAURUS *Merriam.*

Bull. Dept. Geol. Univ. Calif. v. 3, no. 21, p. 419.

Type species, *Thalattosaurus alexandrae.*

Posterior mandibular teeth, broad-elliptical in cross-section, low-crowned; median teeth increasing in height anteriorly through the development of an antero-external tubercle. Anterior mandibular and premaxillary teeth slender conical. Maxillary teeth conical in one species, imperfectly known in the others. Humerus short, expanded distally, with high pectoral ridge. Radius and ulna much shortened.

Thalattosaurus alexandrae *Merriam.*

PLATES I, II; PLATE IV, FIG. 1; PLATE V, FIGS. 1*a*-2*b*; PLATE VI; PLATE VII, FIGS. 1-3, 8-9; PLATE VIII, FIGS. 1-2, 4*a*-6.

Bull. Dept. Geol. Univ. Calif. v. 3, no. 21, p. 419.

Type specimen No. 9085 Univ. Calif. Palae. Coll.

This is the largest species of the group. The known specimens appear to represent individuals attaining a length not far from two metres. Neural spines of vertebrae not greatly widened. Propodial and epipodial limb elements and scapula considerably expanded. Nasal openings long, portion of nasal elements behind the nares relatively short. Slender anterior teeth with widely spaced striae. Posterior mandibular teeth very low-crowned, button-like. The number of teeth on the dentary appears to have been eighteen.

A large part of our knowledge of the Thalattosauria has been obtained through the study of this species, of which several representative specimens are known. All of the material representing this form has been obtained in the Trachyceras horizon of the Hosselkus Limestone. No occurrences are known outside the Shasta region of California.

MEASUREMENTS.

Vertebrae.

		mm.
Anterior dorsal (No. 9084),	height of centrum	20
" " "	width " "	23
" " "	length " "	16
" " "	height of upper arch	46
" " "	antero-posterior diameter of upper arch at middle height of spine	13
" " "	transverse diameter of upper arch at middle height of spine	[1]*a*5
Anterior caudal (No. 9085),	height of centrum	30
" " "	width " "	13
" " "	length " "	18
" " "	height of upper arch	48
" " "	antero-posterior diameter of upper arch at middle height of spine	8
" " "	transverse diameter of upper arch at middle height of spine	6

[1]*a*, approximate.

Arches.

Coracoid (No. 9085), antero-posterior diameter	65
" " transverse diameter of median portion	33
Scapula " greatest length	55
Ischium (?) " " "	72
" " " width	26.5
Pubis (?) (No. 9044), " length	106
" " " width	47

Limbs.

Humerus (No. 9084), greatest length	75
" " " width, proximal end	39
" " " " median portion	21
" " " " distal end	52
" " " thickness of distal end	18.5
Radius " " length	[1]*a*40
" " " width, distal end	*a*29
" " " " median portion	15.5
Ulna (No. 9085), greatest length	40
" " width, median portion	25

Thalattosaurus shastensis, n. sp.

Plate III; Plate IV, Figs. 2*a–c;* Plate VII, Figs. 4, 7; Plate VIII, Figs. 3, 7, 8

Type specimen No. 9120 Univ. Calif. Palae. Coll.

Compared with *T. alexandrae* the individuals are considerably smaller; the scapula, humerus and ulna more slender; the nasal openings shorter and that portion of nasal bones behind the openings longer and broader; the neural spines of the dorsal vertebrae are possibly shorter. The conical teeth associated with the type specimen show more numerous and more closely set longitudinal striae than are seen in the jaw teeth of *T. alexandrae.* There is of course a possibility that these teeth belong to the pterygoids and not to the jaws.

This species appears to be very near the type form of the genus and may be shown later to be identical with it, possibly representing young individuals. There are, however, several specimens in the collection which seem to have the same characters and to be slightly removed from *T. alexandrae.*

This form is not uncommon, and ranges from the Trachyceras horizon almost if not quite to the top of the Hosselkus Limestone. It is known only from the Triassic of Shasta County.

[1] *a*, approximate.

Measurements.

	mm
Humerus (No. 9120), length	32
Ulna " "	21
" " greatest width	11

Thalattosaurus perrini, n. sp.

Plate IV, Fig. 3; Plate V, Fig. 3; Plate VII, Fig. 6.

Posterior mandibular teeth with laterally compressed and obtuse but not greatly depressed crowns, grading anteriorly into a slender conical form on the anterior portion of the jaw. Maxillary teeth slender conical, set in deep pits.

The dentition of the dentary and the maxillary are well shown. The dentary holds an interrupted series of twelve teeth with spaces for several more among them. The entire number has probably been sixteen to eighteen. The posterior ones have low, broad, laterally compressed crowns. The individuals in the middle of the series were short, broad, and leaf-like, their margins being very close together. The anterior members of the series have a shorter antero-posterior diameter, higher crowns, and a slender conical form without lateral compression. The most anterior tooth, seen only in oblique section, shows strong longitudinal striations or ridges on its surface. The most posterior teeth are close together and in shallow pits. The anterior ones are deeply set and are more widely spaced.

On the maxillary there are five teeth of slender conical form, with spaces for one or two more. They are in deep, distinct pits.

As much of the vomerine dentition as is known is very similar to that of *Thalattosaurus alexandrae*.

The general characters of this form are those of a typical Thalattosaurian.

The type specimen, the only known specimen of this species, was the first Thalattosaurian discovered. It was found by Professor James Perrin Smith in the Trachyceras beds of the Hosselkus Limestone at Smith Cove, near Squaw Creek, Shasta County. There was exposed on the slab only a prevomer with its peculiar, blunt teeth. Later the portion of the skull shown on Plate IV, figure 3 was exposed by preparation with steel points and by etching with very dilute hydrochloric acid. After the jaws had been partly uncovered, the writer published a note on the Triassic Reptilia from Northern California,[1] in which this specimen was referred to as a *Shastasaurus* with a heterodont dentition. Later it was discovered that it could not belong to the Ichthyosauria, but the true affinities were not known until after the discovery and study of the type of *Thalattosaurus alexandrae*.

[1] Science, n. ser. v. 15, p. 411.

This species is quite distantly removed from *T. alexandrae* in dental characters, and may be found to represent a distinct genus.[1] Although the posterior mandibular teeth differ much from those of *T. alexandrae* the difference is only one of degree. So far as known the character of the maxillary teeth seems to be quite different both as regards form and insertion. Satisfactory comparison can not be made, however, until we know more of the dentition of *T. alexandrae*.

NECTOSAURUS, n. gen.

Nectosaurus halius, n. gen. and sp.

PLATE IV, FIG. 4*a*-5; PLATE V, FIGS. 4, 6; PLATE VII, FIG. 5.

Type specimen No. 9124 Univ. Calif. Palae. Coll.

Fronto-parietal region similar to that of *Thalattosaurus*. Quadrate with exterior wing. Mandible of lacertilian type. Crowns of posterior mandibular teeth conical, acute, slightly recurved, coarsely striated.

To this species are referred a portion of a skull constituting the type, and a number of isolated bones which seem to belong here. The type was the first thalattosaurian specimen to be carefully studied. Manuscript was originally prepared for its description as a primitive Lacertilian but was withheld from publication until more material should be obtained.

While the mandible and quadrate are of a lacertilian type, thalattosaurian affinities are indicated by the character of the fronto-parietal region. The frontals (Pl. IV, fig. 4*a*) have the same form as in *Thalattosaurus*. They receive the premaxillaries between them anteriorly, and clasp the parietals posteriorly. There is also present a portion of a prefrontal and a post-fronto-orbital. A cross-section of a vertebra (Pl. VII, fig. 5) shows the upper arch apparently firmly connected with the centrum.

This genus contains the most primitive forms of the Thalattosauria and will probably furnish additional evidence concerning their relationships when its skeletal structure is better known.

N. halius appears to be present at nearly all horizons of the Hosselkus Limestone.

In Plate V, figure 6, there is shown a small jaw representing a type quite common in the Hosselkus Limestone. While not seen in association with certainly recognizable *Nectosaurus* remains, it is doubtfully referred to that genus. The dentigerous palatal element shown in Plate V, figure 4 is still more doubtfully determined as belonging here.

[1] Should this type be found to be generically distinct from *Thalattosaurus* the generic name *Scenodon* will be used to distinguish it.

EXPLANATION OF PLATE I.

Thalattosaurus alexandrae.

Type specimen. All figures three fourths natural size.

Fig. 1. Anterior portion of cranium and mandible. Cranium slightly distorted, the anterior end of the maxillary being covered.

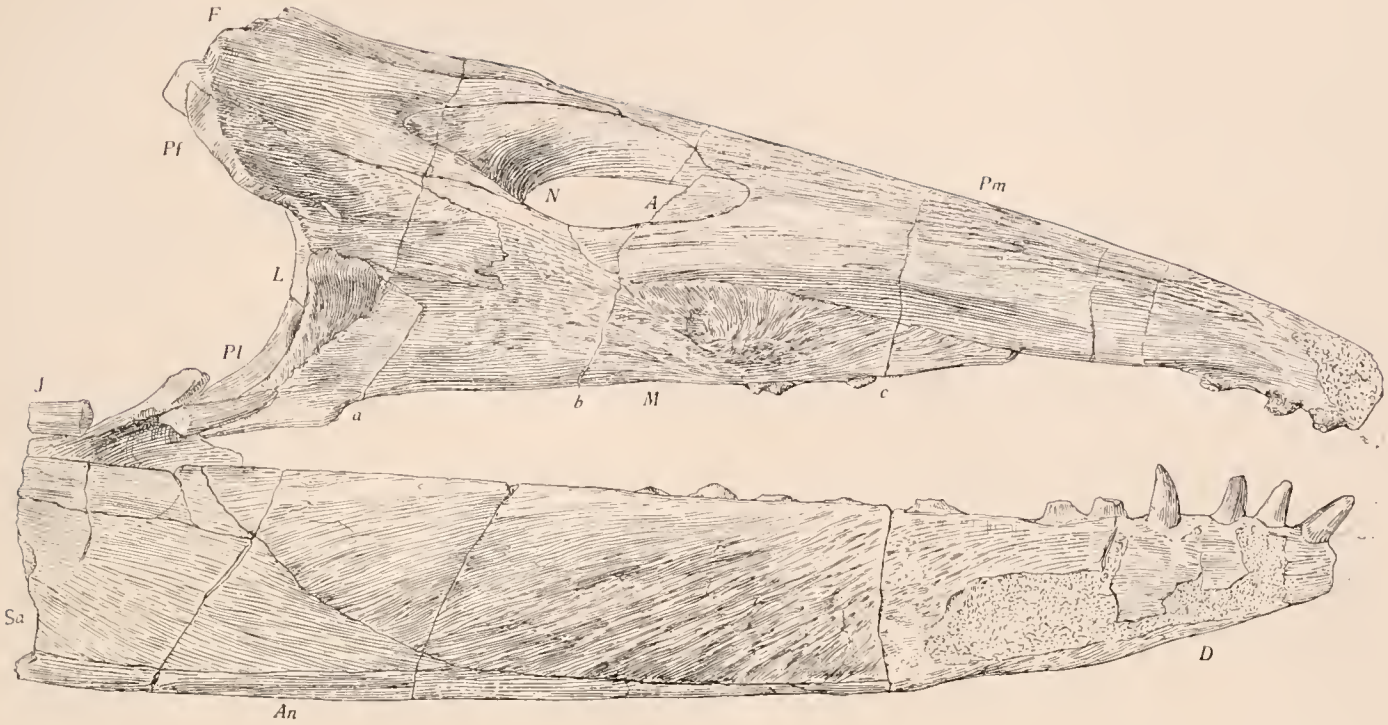
Fig. 2. Palatal view of cranium.

Fig. 3. Inner side of mandible.

LEGEND.

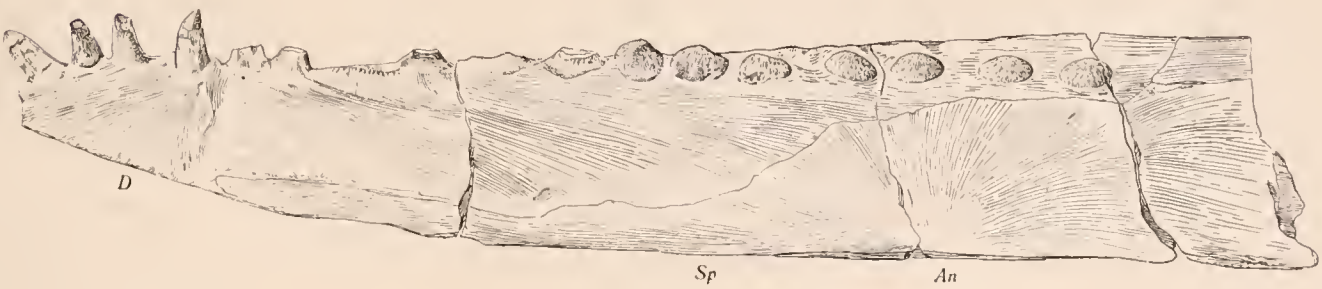
F, frontal
Pf, prefrontal
N, nasal
A, doubtful element anterior to narial opening
Pm, premaxillary
M, maxillary
L, lachrymal
Pl, palatine
J, jugal
V, prevomer
I, inferior narial opening
Sa, supra-angular
An, angular
D, dentary
Sp, splenial
a, *b*, *c*, sections of cranium. See Pl. II, figs. 1*a*, 1*b*, 1*c*.

N and *A* in fig. 1 are situated in the superior narial opening.



1

2



3

EXPLANATION OF PLATE II.

Thalattosaurus alexandrae.

All figures three fourths natural size.

Fig. 1*a*. Section *a* through cranium of type specimen, posterior to superior nares. See Pl. 1, figs. 1 and 2, section *a*.

Fig. 1*b*. Section *b* through cranium of type specimen, anterior portion of superior narial region. See Pl. 1, figs. 1 and 2, section *b*.

Fig. 1*c*. Section *c* through cranium of type specimen, middle rostral region. See Pl. 1, figs. 1 and 2, section *c*.

Fig. 2*a*. Right quadrate, inner side.

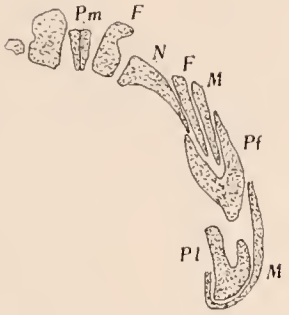
Fig. 2*b*. Right quadrate, outer side.

Fig. 3. Posterior end of premaxillary. *T. alexandrae* (?)

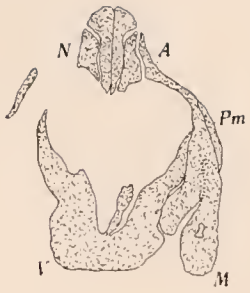
Fig. 4. Fragment of quadrate and temporal region of type specimen.

LEGEND.

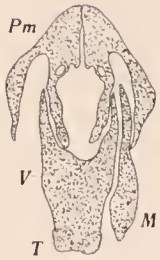
M, maxillary
Pm, premaxillary
N, nasal
F, frontal
Pf, prefrontal
A, doubtful element anterior to narial opening
Pl, palatine
V, prevomer
T, tooth
Q, quadrate
Sq, squamosal



1a



1b

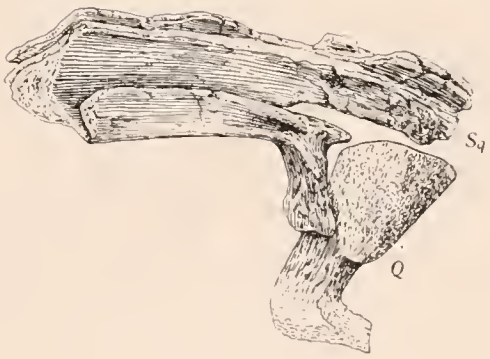


1c

2a

2b

3



4

EXPLANATION OF PLATE III.

Thalattosaurus shastensis.

All figures three fourths natural size.

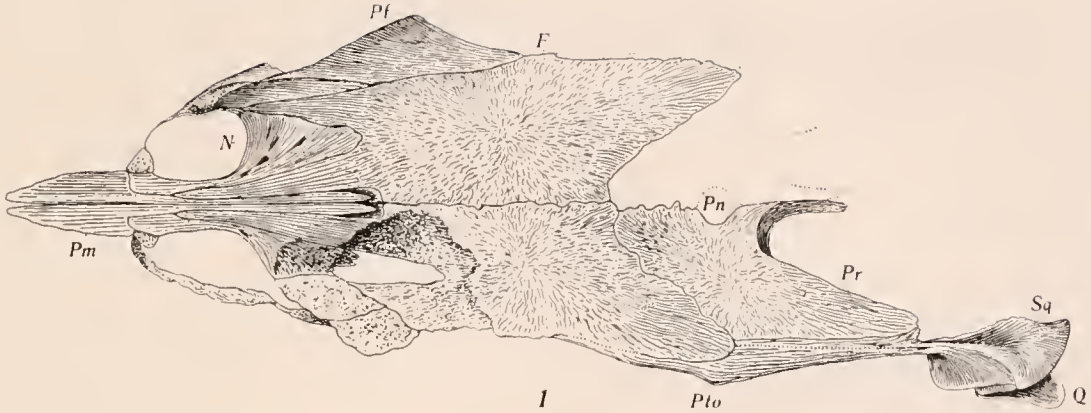
Fig. 1. Superior view of cranium.

Fig. 2. Lateral view of cranium and mandible.

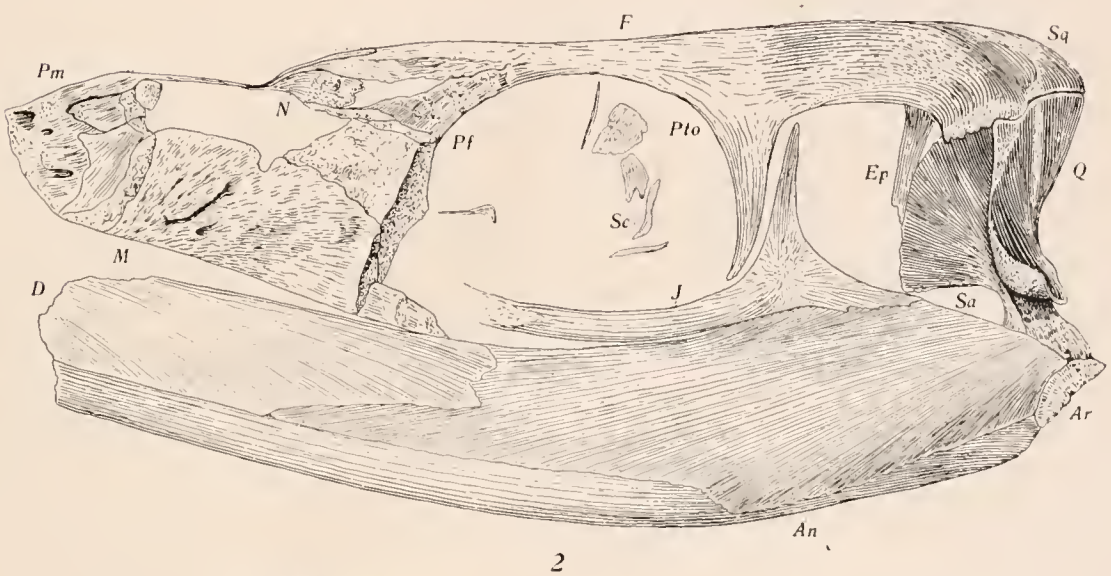
Fig. 3. Lateral view of skull from right side.

LEGEND.

M, maxillary
Pm, premaxillary
N, nasal
F, frontal
Pr, parietal
Pn, pineal foramen
Pf, prefrontal
Pto, post-fronto-orbital
Ptg, groove for post-fronto-orbital
J, jugal
Sc, sclerotic plates
Sq, squamosal
Q, quadrate
Ep, epipterygoid (?)
Pl, palatine
V, prevomer
Ar, articular (?)
An, angular
Sa, supra-angular
D, dentary
Sp, splenial


Pf
F
N
Pn
Pm
Pr
Sq
Q
Pto

1


F
Sq
Pm
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Sc
M
D
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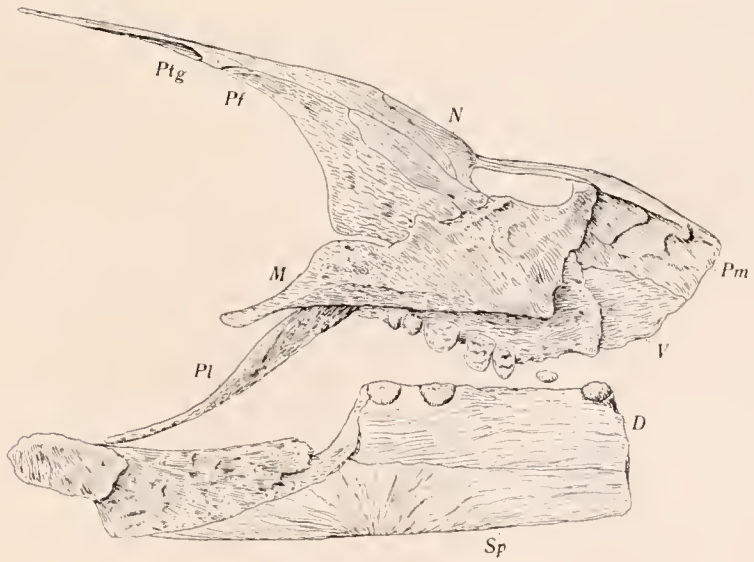
Sa
Ar
An

2


Ptg
Pf
N
M
Pm
V
Pl
D
Sp

3

EXPLANATION OF PLATE IV.

Fig. 1. Anterior jaw tooth associated with type specimen of *T. alexandrae*. × 1½.

Fig. 2*a*. *Thalattosaurus shastensis*. Inner side of right half of cranium and mandible. Type specimen. × ¾.

Fig. 2*b*. Tooth associated with skull of *T. shastensis* shown in fig. 2*a*. × 2.

Fig. 2*c*. Tooth associated with skull of *T. shastensis* shown in fig. 2*a*. × 2.

Fig. 3. *Thalattosaurus perrini*. Inner side of right half of cranium and mandible. Type specimen. × ¾.

Fig. 4*a*. *Nectosaurus halius*. Superior aspect of fragment of cranium. Type specimen. × ¾.

Fig. 4*b*. *N. halius*. Inner side of right ramus of mandible. Type specimen. × ¾.

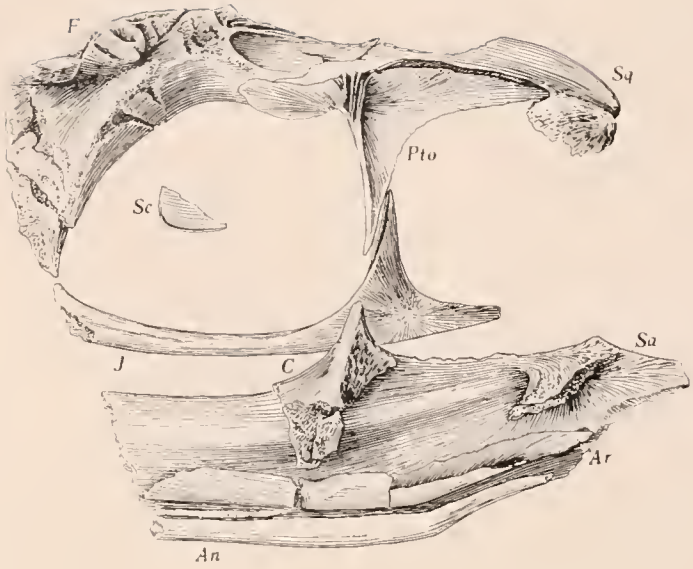
Fig. 4*c*. *N. halius*. Outer side of middle portion of left ramus of mandible. Type specimen. × ¾.

Fig. 5. *N. halius*. Outer side of right ramus of mandible. × ¾. The anterior end of the supra-angular has been weathered through.

LEGEND.

D, dentary
C, coronoid
An, angular
Sa, supra-angular
Ar, articular
Sp, splenial
F, frontal
Pf, prefrontal
Pto, post-fronto-orbital
Sc, sclerotic plate
J, jugal
Pr, parietal
Sq, squamosal
Q, quadrate
M, maxillary
Pl, palatine
a, prefrontal (?)
b, frontal (?)

1



2a

2b

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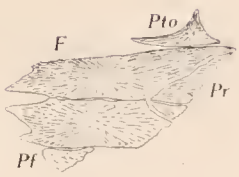

4a

4c

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5

EXPLANATION OF PLATE V.

Fig. 1*a*. *Thalattosaurus alexandrae*. Pterygoid, lateral view. Type specimen. Natural size.

Fig. 1*b*. Upper side of specimen shown in fig. 1*a*. Natural size.

Fig. 1*c*. Lower side of specimen shown in fig. 1*a*. Natural size.

Fig. 2*a*. *Thalattosaurus alexandrae*. Lower side of prevomer. × ¾.

Fig. 2*b*. Lateral view of specimen shown in fig. 2*a*. × ¾.

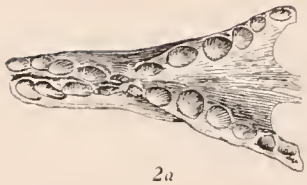
Fig. 3. *Thalattosaurus perrini*. Lateral view of prevomer. Median pair of teeth partly restored. Type specimen. × ¾.

Fig. 4. *Nectosaurus halius* (?) Pterygoid or palatine, superior view. × 1½.

Fig. 5. *Thalattosaurus*, sp. Vomerine tooth. × 1½.

Fig. 6. *Nectosaurus halius* (?) Maxillary. Natural size.

1a



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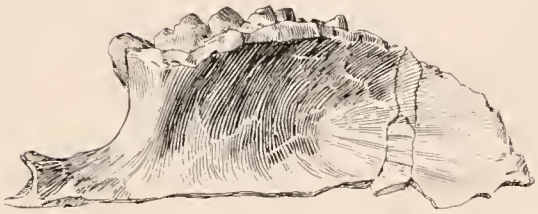
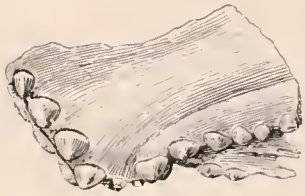


1b



2b

1c

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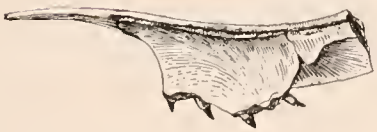

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EXPLANATION OF PLATE VI.

Thalattosaurus alexandrae.

Reconstruction of the skull.

About one half natural size.

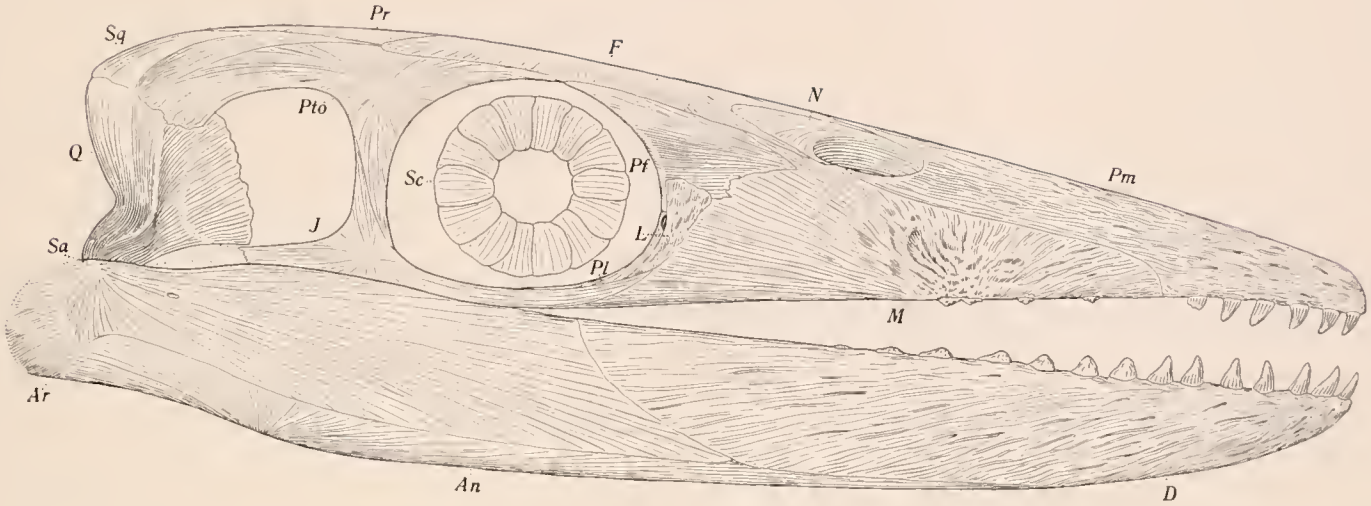
Fig. 1. Lateral view.

Fig. 2. Superior view.

The temporal and fronto-parietal regions and a portion of the mandible are restored from *T. shastensis.*

LEGEND.

Pm, premaxillary
M, maxillary
N, nasal
F, frontal
Pr, parietal
Pn, pineal foramen
Pf, prefrontal
Pto, post-fronto-orbital
J, jugal
L, lachrymal
Pl, palatine
Sc, sclerotic ring
Sq, squamosal
Q, quadrate
Ar, articular
Sa, supra-angular
An, angular
D, dentary



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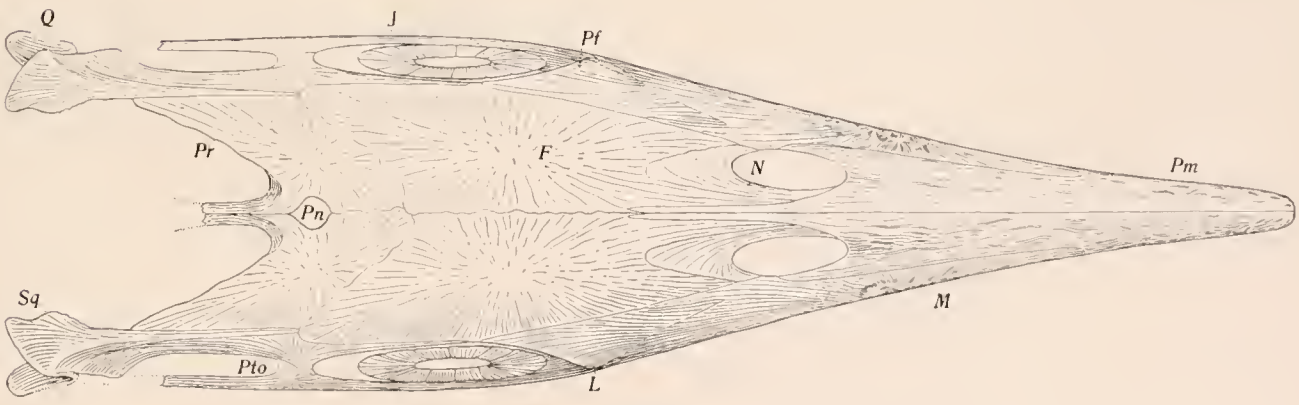


2

EXPLANATION OF PLATE VII.

All figures three fourths natural size.

Fig. 1. *Thalattosaurus alexandrae.* Anterior dorsal vertebra, side view.

Fig. 2. *T. alexandrae.* Dorsal vertebra, anterior side.

Fig. 3. *T. alexandrae.* Anterior caudal vertebra, side view and sagittal section. The neural spine appears to be somewhat too erect in the figure. Type specimen.

Fig. 4. *T. shastensis.* Neural arch of a cervical or anterior dorsal vertebra. Type specimen.

Fig. 5. *Nectosaurus halius.* Weathered cross-section of vertebra. Type specimen.

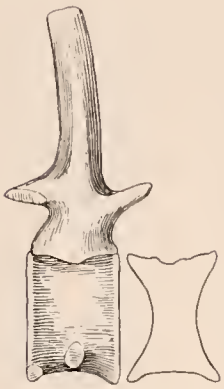
Fig. 6. *Thalattosaurus perrini.* Anterior dorsal rib. Type specimen.

Fig. 7. *T. shastensis.* Head of dorsal rib. Type specimen.

Fig. 8. *T. alexandrae.* Pubis (?)

Fig. 9. *T. alexandrae.* Ischium (?) Type specimen.

Fig. 10. *T. alexandrae.* Pubis (?)



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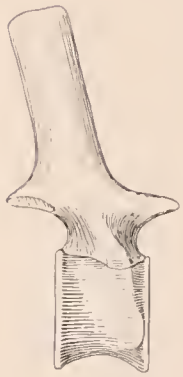

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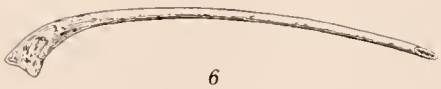

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EXPLANATION OF PLATE VIII.

All figures three fourths natural size.

Fig. 1. *Thalattosaurus alexandrae.* Coracoid. Type specimen.
Fig. 2. *T. alexandrae.* Scapula. Type specimen.
Fig. 3. *T. shastensis.* Scapula. Type specimen.
Fig. 4*a*. *T. alexandrae.* Left humerus, superior view.
Fig. 4*b*. Inferior view of specimen shown in fig. 4*a*.
Fig. 5. *T. alexandrae.* Radius.
Fig. 6. *T. alexandrae.* Ulna. Type specimen.
Fig. 7. *T. shastensis.* Ulna. Type specimen.
Fig. 8. *T. shastensis.* Humerus. Type specimen.

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4a

4b

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